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Coping with Changing Northern Environments: The Role of the Stress Axis in Birds and Mammals[1]

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SYNOPSIS. Northern environments present ecological and physiological problems for homeotherms that require adaptations to cope with severe and less predictable physical factors while at the same time continuing to have to cope with the biological ones, such as competition and predation. The stress axis plays a central role in these adaptations and I discuss the range of solutions that birds and mammals have evolved. The stress response in these animals is not static when a challenge occurs, but may be modulated depending on the biological function during the annual cycle (breeding versus nonbreeding), either under-responding to permit reproduction (some song birds) or responding vigorously, yet not having this compromise reproduction (Arctic ground squirrels). Both may trade off survival for reproduction. In contrast, the snowshoe hare shows the expected stress response to chronic high predation risk over 2–3 years: body resources are geared to survival and reproduction is inhibited. Two long term, persistent, and pervasive changes will confront northern birds and mammals in the 21st century: global change and persistent organochlorine pollutants (POPs). These may result in either adaptations or shifts in distribution and abundance. For the former, latitudinal variation in the stress axis may help song birds respond rapidly; population variation in the stress axis response is unknown in northern mammals and relatively sedentary mammals may be unable to shift their distribution rapidly to adjust major climate shifts. For the latter, the few POPs studies that have examined the stress axis indicate marked negative effects.

INTRODUCTION

The severity and unpredictably of higher latitude and alpine habitats present special challenges to birds and mammals who live out some or all of their lives there. These habitats are characterized by short summers with a burst of primary productivity separated by long winters with permanent snow cover. Habitat has been regarded as the template that constrains and shapes the evolution of successful physiological and ecology strategies (Southwood, 1988). Though it cannot be the sole determinant for any particular suite of traits, habitat clearly plays a central role. The neuroendocrine system is a major pathway that integrates environmental change and through which life history decisions to reproduce, to grow, or to put energy into storage are implemented in the face of environmental uncertainty. It is thus a critical component adapting organisms to northern habitats and should be under strong selection pressure to evolve successful strategies which may be unique to these environments (Finch and Rose, 1995).

The limbic system (dentate gyrus and hippocampus) and the hypothalamic-pituitary-adrenocortical axis (HPA) are pivotal components of the neuroendocrine system coordinating successful adaptation to habitat for three reasons. I refer to these two components together as the stress axis as they play an integrated role through regulation and feedback (Fig. 1) that is, depending on the situation, permissive, suppressive, or stimulatory (Sapolsky *et al.*, 2000). First, the stress axis is a critical one involved in normal day-to-day activities associated with the diurnal cycle of waking such as increased locomotion, exploratory behavior, increased appetite, and food-seeking behavior (reviewed in McEwen *et al.*, 1988; Wingfield and Romero, 2001). Second, the stress axis permits short-term adaptation to maintain survival in the face of acute, environmental stressors. The term ''stress'' tends to be a vague, inclusive one, but here I use it informally as the general state of stressors that provoke a stress response (Selye, 1971; Sapolsky, 2002). The stress response is that set of responses by birds and mammals to potentially harmful environmental challenges (stressors). This response can be rapid and short-term—the classic ''flight or fight'' syndrome—that takes seconds to minutes to develop and is a generalized response to a wide variety of stressors. The response can also play a role coordinating longer duration responses (minutes to hours)—the emergency life history stage—that involves an interruption of the life history cycle currently underway (*e.g.*, reproduction) and redirects physiology and behavior toward survival (Wingfield *et al.*, 1998). The stress response can be activated by environmental stressors such as bouts of severe weather (*e.g.*, Romero *et al.*, 2000), by physical stressors such as attacks by a conspecific or a predator (*e.g.*, Girolami *et al.*, 1996; Hirschenhauser *et al.*, 2000), or by psychological stressors such as the fear of an imminent attack (*e.g.*, Boonstra *et al.*, 1998; Korte, 2001). Though I focus on the stress axis here, it is only one part of the stress response and other hormones, neurotransmitters, opioid peptides, cytokines and brain functions are also rapidly called into play (Sapolsky *et al.*, 2000). Third, the axis is central to certain long-term evolutionary adaptations to particu-

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lar ecological and habitat pressures such as those encountered in the north (*e.g.*, Boonstra *et al.*, 2001; Wingfield and Hunt, 2002). Reproduction or survival may be maximized by evolving a stress response that is modulated by under-responding to a stressor or that is sustained chronically in spite of its negative consequences.

My objective in this paper is to give an overview of what is known about how environment-dependent modifications of the stress axis and its response adapt birds and mammals to survive and succeed in northern environments. Thus I will not discuss aspects of the axis that are common to all environments. The topic of stress physiology and the brain is enormous and complex, ranging from the cellular and molecular to the whole organism. For greater detail, a number of comprehensive sources can be consulted (*e.g.*, Silverin, 1998; Sapolsky *et al.*, 2000; McEwen, 2001; Wingfield and Romero, 2001). I focus on species that reproduce at higher latitudes (Arctic and boreal regions) and on those that overwinter at latitudes where snowfall characterizes winter habitats (temperate, boreal, and Arctic regions). I do this for three reasons. First, the physiological adaptations of well-studied species from lower-latitude regions (temperate and boreal) may have applicability to those living further north. Second, there is a paucity of endocrinological information on how the axis functions in many northern species, even those with wide distributional ranges, and we need to highlight this gap in knowledge and redress it. Much of what we know about how the axis functions normally and in response to stressors is based on a very limited subset of mammals, especially laboratory rodents, and a slightly larger subset of birds (Romero, 2002). Third, as global climate change and the movement of persistent organic pollutants is likely to have a dominant effect on the distribution and abundance of species in the north in the 21st century we need an understanding of the current adaptations of northern species and of their capacity for change. Finally, research on the HPA axis in natural populations of birds has been much more intensive than that in mammals, particularly in the north, and it is apparent that there is extensive variation amongst species in response to similar ecological problems: more than one solution appears to work. The research documenting this complexity has been the subject of a number of recent reviews (Silverin, 1998; Wingfield and Hunt, 2002; Wingfield and Silverin, 2002), and I will discuss only some of the broad patterns for this group.

THE STRESS RESPONSE

An external stressor sets off a rapid cascade of responses in vertebrates to deal with the threat and then to reestablish homeostasis (Sapolsky *et al.*, 2000). I will discuss the major changes that occur in stress axis of mammals (Fig. 1), though that in birds is similar (Harvey *et al.*, 1984; Silverin, 1998). Within seconds of the stressor, the sympathetic nervous system causes the adrenal medulla to release catecholamines (epinephrine and norepinephrine) into the general circulation and the paraventricular nucleus (PVN) of the hypothalamus releases primarily corticotropic releasing hormone (CRH), but also arginine vasopressin

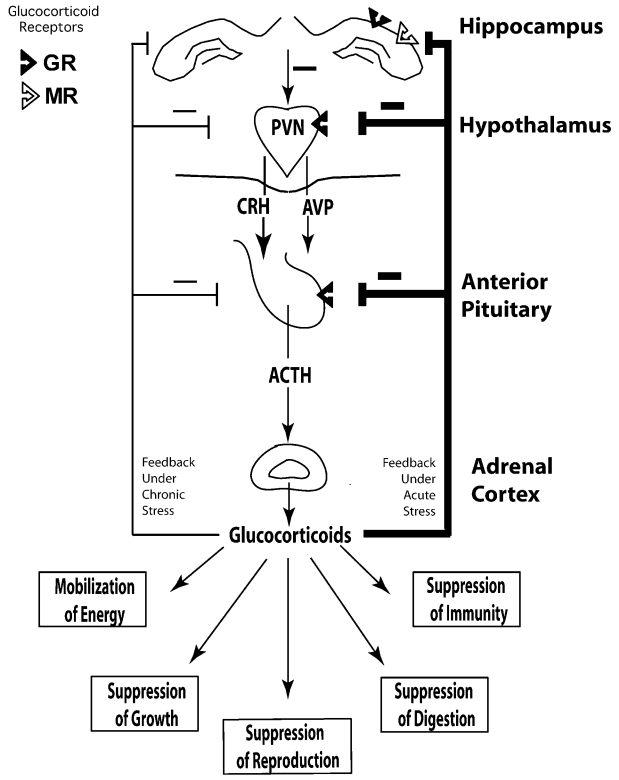

FIG. 1. The hippocampus and the hypothalamic-pituitary-adrenal (HPA) axis, the major impacts on body processes, and the glucocorticoid (GC) feedback in the mammalian brain. The hippocampus regulates the overall functioning of the HPA. A stressor causes the hypothalamic paraventricular nucleus (PVN) to release corticotropin releasing hormone (CRH) and vasopressin (AVP), which causes the anterior pituitary to release adrenocorticotrophin (ACTH). ACTH initiates the synthesis and release of glucocorticoids (GCs, corticosterone in some rodents, cortisol in others) from the adrenal cortex. GCs act at multiple sites within the body to maintain homeostasis, but because of the damaging effects of extended exposure to GCs, the HPA axis is tightly regulated through feedback (inhibition indicated by -) on glucocorticoid receptors to inhibit further HPA activity. Cortisol feeds back on hypothalamus and pituitary to cause a rapid inhibition of CRF release. Under conditions where the stressor is acute, feedback mechanisms operate efficiently and the system rapidly returns to normal, resulting in effects on body processes that are only short-term. Under conditions where the stressor is chronic, feedback signals are weak and the system remains activated for longer periods, resulting in effects on body processes that can be long term and detrimental. Short-term effects result in suppressive impacts on body processes; long-term chronic effects result in inhibitory impacts on body processes. Glucocorticoid (GR) and mineralocorticoid receptors (MR) occur in the limbic system (hippocampus and dentate gyrus) and GR occur in the PVN and anterior pituitary. In the brain, MR have a higher affinity than do GR for GCs, and at basal concentrations of cortisol, MR are occupied whereas GR remain largely unoccupied. During periods of stress and elevated plasma GCs, there is increased occupation of GR. Hippocampal MR may be primarily involved in feedback regulation during basal secretion, whereas GR become important during periods of increased GC secretion (from de Kloet *et al.*, 1999; Matthews, 2002; Sapolsky, 2002).

(AVP), into the portal system. These cause the anterior pituitary to release adrenocorticotropic hormone (ACTH) into the general circulation. In response to the ACTH, the adrenal cortex releases glucocorticoids (GCs) within minutes into the general circulation. In birds and some small mammals (bats, voles, and mice) the primary GC is corticosterone and in other mammals it is cortisol or a mixture of cortisol and corticosterone (*e.g.,* hares, squirrels, primates, ungulates). The response results in mobilizing and shunting of energy to muscles by stimulation of hepatic gluconeogenesis (the production of glucose) and away from peripheral tissues not needed for short-term survival. Cardiovascular tone is increased, immune function is stimulated, inflammatory response is suppressed, pain preception is blunted, reproductive physiology and behavior inhibited, feeding and appetite is decreased, and cognition is sharpened. Under conditions where the stressor is acute, GCs exert feedback at three levels in the brain (Fig. 1) to return the body back to pre-activation state. Key to this feedback are the intracellular GC receptors (MR—mineralocorticoid receptors and GR—GC receptors) in the critical brain areas (Fig. 1) (de Kloet *et al.,* 1999).

The stress response and the homeostatic set-point are not fixed, species-dependent characteristics, but are modified by the annual pattern of life history changes, by development, by energy reserves, and by experience. First, over the annual cycle of northern homeotherms, the requirements of reproduction, migration, and coping with winter may require that the stress axis be modulated in different ways at different times to optimize reproduction, survival, or both in the face of environmental challenges. This modulation has been referred to as allostasis (*i.e.,* achieving stability through change—McEwen and Wingfield, 2003). Challenges that are recurrent and predictable (*e.g.,* intense, direct male-male aggression associated with the breeding or bouts of severe weather on the breeding grounds in spring), would, if the species did not evolve a modifying solution, inhibit reproduction. Neither basal GC concentrations nor the response to stressors remain constant over the annual cycle and changes in the two are not necessarily closely correlated (*e.g.,* baseline concentrations may be high at some times, but response to a stressor dampened—for an overview, see Romero, 2002). This is consistent with the laboratory evidence that indicates that there is differential regulation of baseline and stress GC concentrations and that these may serve different physiological and ultimately ecological functions (de Kloet *et al.,* 1999; Sapolsky *et al.,* 2000).

Second, during the critical pre- and postnatal periods of development, maternal effects may alter the phenotype of the progeny (Bernardo, 1996; Mousseau and Fox, 1998). This can happen in both birds (Royle *et al.,* 2001) and mammals (*e.g.,* Festa-Bianchet *et al.,* 2000). In mammals, the developing stress axis is particularly vulnerable to such early experiences and can result in life-long programming of the stress response and homeostatic control (Matthews, 2002). There is also an interplay between changes in the HPA axis and the reproductive axis, which will ultimately translate in to changes in adult fitness.

Third, experience may alter the HPA axis response. This axis functions well when the stressor is of short duration (minutes to hours); thereafter the pronounced negative, inhibitory effects of chronic stress start becoming evident and intensify. Laboratory evidence in rodents indicates that the ACTH response is desensitized when the animal is repeatedly exposed to certain types of stressors (*e.g.,* cold exposure), but not to others (*e.g.,* footshock—Aguilera, 1998) but that entirely new stressors continue to elicit a typical stress response. Under conditions where the stressor becomes chronic (days to months), the suppressive effects of GCs grade into inhibition (Fig. 1), with the resulting impacts being potentially deleterious, affecting long-term survival and fitness through infertility, impaired resistance to disease, and inhibition of growth. Chronic stress may have two long-lasting effects that cause animals to secrete higher GC concentrations than normal in response to ACTH. First, the hippocampus affects the response of the HPA to stressors by negative feedback regulation and chronic stress will reduce this regulation by causing a down regulation of GC receptors in the hippocampus, with the effect that GC concentrations rise (*e.g.,* Webster and Cidlowski, 1994; Meyer *et al.,* 2001). Second, chronic stress can cause adrenal hypertrophy, increasing the productive capacity of the adrenocortical tissue (Miller and Tyrrell, 1995), resulting in an enhanced production of GC.

Methods to assess the stress axis

There are three major methods to assess the status of the stress axis in natural populations. First, GC concentrations can be determined from different categories of animals before and after the application of a stressor and their concentrations compared (*e.g.,* before and after hunting). The results allow between category comparisons, but this gives insight only into the overall potential impact of the stressor. Second, the urine or feces of animals can be collected in the field and concentrations of GC metabolites measured (*e.g.,* Palme *et al.,* 1997; Teskey-Gerstl *et al.,* 2000; Wasser *et al.,* 2000). This simple, noninvasive method gives an integrated index of what the animals were experiencing sometime prior to defecation. However, it may be a rough index if sex, rank, and individual identification are unknown. In addition, since GC concentrations show a pronounced circadian rhythm (Dallman *et al.,* 1990), being highest at the onset of daily activity and the lowest at the end of it, concentrations will also be affected by when they are produced in the daily cycle. Since it is usually not possible to know over what period the feces or urine were produced, this may complicate the interpretation. As well, it may not be possible to know what an animal was experiencing during the period the urine or feces were being produced (*i.e.,* was it stressed or not, and if so, for how

long). This would increase variability among samples. Thus the results may only allow one to make general statements about the stress status of entire populations. However, detailed knowledge of the individuals producing the feces or urine (*i.e.,* through knowledge of social status, behavior, sex, etc.), calibration of fecal levels with plasma levels, and standardization of collection techniques, mitigate these limitations (Creel *et al.,* 2002).

Third, a challenge protocol uses a standardized stressor as an index of an animal's ability to respond to natural stressors. Two basic approaches have been used—a capture-challenge protocol and a hormonal-challenge protocol. The capture-challenge protocol uses the capture of the animal as the stressor and typically proceeds as follows. Within 3 min of capture, a baseline blood sample is taken. Timing is critical as the stress response is so rapid that GC concentrations may begin to increase within 3–5 min of capture (*e.g.,* mammals—Seggie and Brown, 1974; birds—Schoech *et al.,* 1991). Thereafter, serial bleeds are taken at regular intervals (*e.g.,* 5, 10, 30, 60 min). This protocol has been preferentially used in birds (see Wingfield and Silverin, 2002) though it also been used in at least one mammal (*e.g.,* Kenagy and Place, 2000). A modification of this protocol was used by Sapolsky (1983) who darted baboons from behind and used their response to the anesthetic as the standardized stressor.

The hormonal-challenge protocol uses a standardized set of injections of hormones or analogues of them that are part of the normal stress response and measures the animal's response over a series of blood samples. This protocol is particularly useful when the techniques of capture exceed the 3 min window and the animal is already stressed. This protocol results in an integrated picture of the animal's recent physiological past (days to weeks) while at the same time overriding the immediate stress response the animal was experiencing because of the effects of capture. It does this both by assessing the responsiveness of the brain to negative feedback back regulation and the capability of the adrenals to respond to a standardized ACTH injection. It typically involves two steps: the dexamethasone suppression test (Kalin *et al.,* 1981) followed by the adrenocorticotropic hormone (ACTH) stimulation test. The dexamethasone suppression test is a method to assess whether the brain is registering high GC concentrations correctly. Dexamethasone is an artificial GC and when injected, negative feedback on the brain should occur, causing a reduced ACTH release from the pituitary, and thus reduced GC production from the adrenals. When dexamethasone resistance occurs (*i.e.,* GC concentrations do not decline as much as expected), it may indicate the animal has been chronically stressed (*e.g.,* Brooke *et al.,* 1994; Hik *et al.,* 2001). However, certain mammal species are naturally dexamethasone resistant (prairie voles—Taymans *et al.,* 1997; *e.g.,* red squirrels—Boonstra and McColl, 2000). The ACTH stimulation test is a method to probe the responsiveness of adrenals directly. When greater than normal GC production occurs, it may also indicate that the animal has been chronically stressed. This protocol, or modifications of it, has been successfully applied in a wide variety of species (*e.g.,* deer—Smith and Bubenik, 1990; sparrows—Astheimer *et al.,* 1994; hares—Boonstra *et al.,* 1998; mockingbirds—Sims and Holberton, 2000).

ADAPTATIONS FOR SURVIVING WINTER

The modulation of the stress response, either by upregulating it or by suppressing it, may be crucial both to preparing for and to surviving winter. Since reproduction is usually restricted to the summer, evolutionary adaptations in winter focus on those that maximize survival. The principal threats to winter survival are starvation and low temperatures, both of which may be aggravated by high predation risk. Terrestrial homeotherms have evolved five major solutions to deal with these threats and the stress axis plays a role in some of these. Though chronically high GC concentrations are generally viewed as ''bad'' for birds and mammals, some of these winter adaptations result in chronically moderate GC concentrations, and thus are ''good'' for survival. However, the pattern is not consistent across all species or groups, particularly among birds, and suggests that there may be more than one evolutionary solution.

First, the majority of northern birds migrate to either tropical regions or to subarctic and northern temperate regions (over 120 species from the Arctic alone, including all passerines and shorebirds, Boyd and Madsen, 1997; Murray, 1998), though some are permanent residents (*e.g.,* ravens, black-capped chickadees, snowy owls). Of the terrestrial mammals, migration is an option only for the larger ones—the barrenland caribou (*Rangifer tarandus*) and their principal predator, the wolf (*Canus lupus*), but these move only to the northern boreal forests (Klein, 1999). The rest of the mammals stay put. Second, decreased metabolic expenditure through hibernation is a strategy employed by chipmunks, ground squirrels, and marmots (Mrosovsky and Sherry, 1980; Nedergaard and Cannon, 1990), coupled with internal fat storage in the last two groups. Third, some birds and mammals cache food to survive winter (Smith and Reichman, 1984). In the northern birds, chickadees, jays, and nuthatches cache seeds and insects, particularly prior to winter. Both pikas in alpine regions and red squirrels in the boreal forest and chipmunks in both alpine and forest regions cache food. The former two species remain active throughout the winter (Obbard, 1987; Dearing, 1997), the latter hibernates and periodically aroses to eat (*e.g.,* Humphries *et al.,* 2001). Fourth, small mammals such as the lemmings, voles, shrews, and weasels require microclimate refugia under the snow to forage and survive and hibernators require significant snow depth to insulate them in their hibernacula. Snow depth may be a critical determinant of survival (*e.g.,* Scott, 1993; Reid and Krebs, 1996; Hubbs and Boonstra, 1997) and subsequent reproduction (*e.g.,* Karels and Boonstra,

2000). Early or delayed onset of snowfall in autumn, snow depth in winter (too much or too little), and delayed snow melt in spring may all be detrimental (Mihok and Schwartz, 1989). Global climate change may affect any or all of these, causing a disjunct between the onset of animal activity in spring and the onset of plant growth (Inouye *et al.*, 2000). Fifth, there can be either a seasonal long-term increase or decrease in body mass and size, as is seen in northern mammals in winter (Ashton *et al.*, 2000) or there can be a daily increase in body mass (fat) and a nightly loss, as is seen in northern wintering birds (Holberton *et al.*, 1999). Bergmann's rule proposes that within a genus of endothermic vertebrates, larger species are found in cooler environments. Though this rule has generated a great deal of controversy, a recent analysis (Ashton *et al.*, 2000) finds support for it in large mammals, but not in smaller ones such as voles and shrews. The latter actually loose weight as winter approaches and maintain low mass throughout winter. The explanation in the larger mammals may be related to heat conservation (larger volume:area ratios in larger individuals), but is more likely related to their greater fasting endurance (Millar and Hickling, 1990). The explanation in smaller mammals may be related to conserving energy by optimizing the minimum body mass required to survive winter. Below I discuss how the stress axis plays a role in some of these.

Migration

Preparation for migration and for winter requires a period of hyperphagia and a laying down of fat reserves (for a review, see Holberton *et al.*, 1999). In birds (Wingfield and Silverin, 1986; Astheimer *et al.*, 1992) and mammals (Dallman *et al.*, 1993), GCs play a vital role in foraging behavior and hyperphagia, with low to moderate concentrations stimulating feeding behavior. Many species of migrating birds show increased baseline concentrations of GCs but a reduced stress response (*e.g.*, O'Reilly and Wingfield, 1995; Ramenofsky *et al.*, 1995). An adaptive explanation for this pattern is the migration modulation hypothesis (Holberton *et al.*, 1996, 1999). It proposes that higher concentrations of baseline GCs are expressed prior to and during migration than at other times to facilitate migratory fattening, but that the stress response is dampened when challenged so that the negative, catabolic effects of high GCs on skeletal muscle do not occur; thus critical skeletal muscles are preserved for flight during migration. This hypothesis has been validated in some studies on birds (Fig. 2A, left panel) (*e.g.*, Holberton *et al.*, 1996; Piersma and Ramenofsky, 1998), but not others. In white-crowned sparrows (Romero *et al.*, 1997), baseline levels were not elevated in fall migrants nor did they show much fattening (Fig. 2A, right panel). Their stress response was similar to that in winter birds. In contrast spring migrants did show both elevated corticosterone secretion and an increase in body fat and this is congruent with

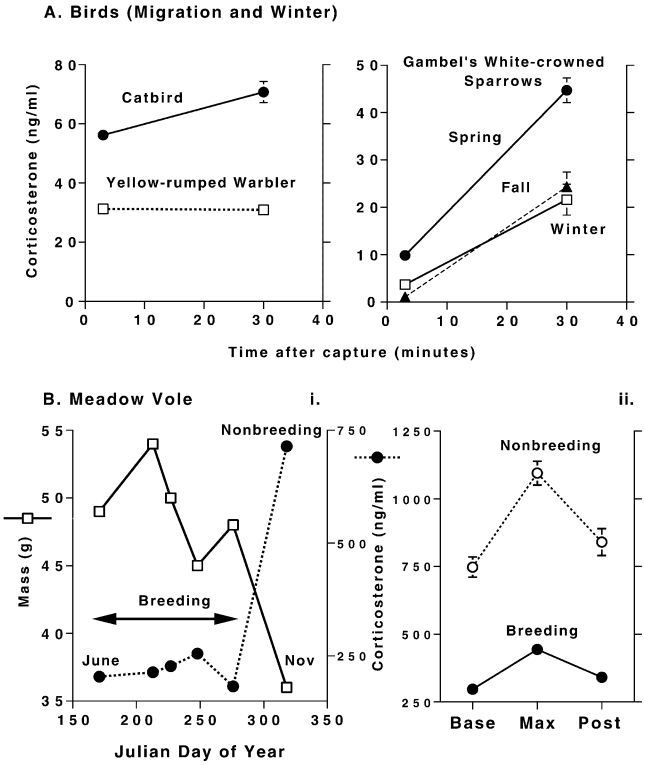

FIG. 2. Glucocorticoids during the nonbreeding season.

A. Corticosterone changes in response to the capture protocol in migrating fall populations of the catbird (*Dumetella carolinensis*) and the Yellow-rumped Warblers (*Dendroica coronota*) (right panel; modifed from Holberton *et al.*, 1996) (means ± 1 SE). These species show high baseline concentrations and a reduced stress response. In contrast, Gambel's White-crowned sparrows (*Zonotrichia leucophrys gambelii*) has low baseline concentrations during the migration fall but high concentrations during the spring migration, with winter concentrations in birds overwintering in New Mexico being similar to those in fall (left top panel). Sparrows at all times continue to respond markedly to the stressor (modified from Romero *et al.*, 1997).

B. Meadow vole (*Microtus pennsylvanicus*)

i. Changes in mass and corticosterone levels of a male 3802 from 20 June to 14 November 1991 from a population near Toronto, Ontario (Boonstra, unpublished). During the first 5 captures, this male was in breeding condition, maintained a mass >44 g and a corticosterone concentration of <250 ng/ml; during the last capture in mid-November, it was not breeding (testes abdominal), body mass had declined 36 g, and corticosterone concentration had increased to >700 ng/ml.

ii. Response of breeding (N = 400) and nonbreeding (N = 79) males from field populations near Toronto (Boonstra, unpublished) to a standardized stressor (Base—blood sample obtained immediately upon release from live-trap after overnight capture; Max—blood sample obtained after 1 hr of restraint in squeeze tube; Post—blood sample obtained after 1 hr recovery after release from tube) (means ± 1 SE). Nonbreeding males had significantly higher levels at all times than breeding males (repeated measures ANOVA) ($F = 613.1$, df 1,477, $P < 0.0001$) and there were significant differences among individuals ($F = 231.6$, df 2,954, $P < 0.0001$) as well as significant interaction effects between individuals and breeding condition ($F = 38.7$, df 2,954, $P < 0.0001$) (see Boonstra and Boag, 1992, for hormone analysis and trapping area and methods).

the hypothesis. Thus different strategies exist to cope with the same general problem.

Differences in energy demand among individuals and between populations may underlie variation in corticosterone secretion during migration as well. In the hermit thrush (*Caltharus guttatus*), a species breeding throughout the boreal forests of North America, migrating individuals in poorer, leaner condition had elevated baseline GC concentrations and a dampened stress response, whereas those in good condition had lower baseline GC concentrations and a normal stress response (Long and Holberton, 2004). A similar relationship between energetic condition and baseline corticosterone and/or adrenocortical response has been found in other studies (*e.g.*, Jenni *et al.*, 2000; but see Piersma *et al.*, 2000; Mizrahi *et al.*, 2001). Between-year variation in condition may directly reflect differences in either severity of the environment or of food availability. The stress response of the spring migrating semipalmated plovers (*Calidris pusilla*), an Arctic breeding species, varied between two years (Mizrahi *et al.*, 2001). Though there was no relationship between baseline GC concentrations and fat levels in either year, plovers were in poorer physical condition (lower fat levels) in the year they also showed a dampened stress response to capture (see also Marra and Holberton, 1998). This may indicate a response to protect the skeletal muscle from high GC concentrations (see also Jenni *et al.*, 2000). Thus the modulation of the stress response is clearly occurring in migrating birds but not all respond in the same way and condition and fat levels may modify the response. Different migratory strategies and other physiological constraints may be the reason for these differences.

Foraging and maintenance of optimal body mass

In winter, food intake in birds and mammals needs to be geared to prevent starvation while at the same time maintaining an optimum body mass to permit rapid escape from predators. GC concentrations may be the critical link between the size of the fat reserves and either environmental severity or predation risk. I will focus first on adaptations in birds and then in mammals.

On days with fresh snowfall, GC concentrations were higher in dark-eyed juncos (*Junco hyemalis*) than on days without fresh snow and fat reserves increased after these snows (Rogers *et al.*, 1993). In England, where winter conditions are milder, great tits (*Parus major*—a species closely related to North American chickadees) used the daily temperature as the proximate cue to assess how much fat to accumulate—the colder the day, the greater the fat accumulated for the coming night (Gosler, 2002). However, a previous study on this species indicated that these fat reserves were not maximized and represented a tradeoff between being fat enough to avoid starvation overnight and being light enough to escape predators such as the sparrow hawk (*Accipiter nisus*) during the day (Gosler *et al.*, 1995).

Body reserves of small and mid-sized mammals that remain active in winter tend to be extremely low and unlikely to be a major energy source. Northern red-backed voles (*Clethrionomys rutilus*) from Alaska always had <1 g of fat, with the body mass in winter being only about 1–2% fat (Zuercher *et al.*, 1999). Snowshoe hares (*Lepus americanus*) in winter also tend to have very low fat levels and are subjected to intense predation pressure for parts of the 10-year cycle (Krebs *et al.*, 2001). In the southern Yukon in February, kidney fat (fat surrounding the kidneys, a prominent storage site) constituted a trivial $0.08\% \pm 0.008$ (1 SE, $N = 226$) of body mass (Boonstra, unpublished). Hares in winter have only sufficient internal reserves to survive 2–4 days without feeding (Whittaker and Thomas, 1983). Thus the voles and hares must forage daily to sustain themselves. Small mammal species at higher latitudes are short lived and in general, highly seasonal breeders. Most live considerably less than one year and virtually no vole that breeds in one year is alive the next (Boonstra, 1994). Thus, the nonbreeding young from one summer must survive winter to become the breeding adult population of the next. Since the onset of aging processes occur with the onset of maturation (Kirkwood and Austad, 2000), the nonbreeding young require adaptations to delay aging during the winter nonbreeding period. Essentially, a significant part of their neuroendocrine system in winter has to be geared to enduring and surviving an environmentally challenging period to permit an opportunity to reproduce in the next breeding season. Most small mammal species living at northern latitudes maintain lower body mass during autumn and winter than they do in summer (*e.g.*, Iverson and Turner, 1974; Hansson, 1990). In laboratory studies, Dark *et al.* (1983) found that meadow voles (*Microtus pennsylvanicus*) lost 20% of their body mass and consumed 30% less food under short photoperiods characteristic of winter conditions. This would reduce both the energy demands and the time needed to forage for it. This lower body mass presumably represents a physiological optimum for winter survival, as voles that are either too small or too large do not survive winter (Aars and Ims, 2002).

I suggest that this winter adaptation may represent the natural equivalent of the best method known to prevent aging in mammals and to extend life in the laboratory-caloric restriction. Caloric restriction, which markedly extends lifespan in laboratory rodents (Ramsey *et al.*, 2000) but also in a wide variety of other species, simultaneously causes a moderate hyperadrenocorticism (Sabatino *et al.*, 1991). Evidence suggests that the latter contributes to retarded aging process (Masoro, 2000). Field evidence in meadow voles (Fig. 2B) indicates that males during the breeding season maintain significantly lower levels of corticosterone than they do during the nonbreeding season, both at baseline concentrations and when stressed by a standardized protocol. Thus, these moderate levels of glucocorticoids during winter may be one of the

adaptations that small mammal species have to survive this period.

Latitudinal gradients and severity of winter

Within a bird species, there may be a latitudinal gradient in HPA sensitivity to unpredictable environmental stressors: those populations wintering further north, where climate is inherently more challenging and less predictable, should exhibit a more pronounced stress response than those living in more stable environments (Rogers *et al.*, 1993; Wingfield *et al.*, 1993; Holberton and Able, 2000). This would allow them to respond more rapidly to stressors such as winter storms. Though there was no difference in baseline GC concentrations between juncos (*Junco hyemalis*) wintering in New York (more severe winters) and those wintering in Mississippi (mild winters), those in New York were fatter and showed a greater amplitude stress response (Holberton and Able, 2000).

Fasting

Prolonged natural fasting is an adaptation by some birds and mammals to periods when food is unavailable, either because it is in short supply or because feeding would disrupt activities of greater importance (*e.g.*, hibernation, incubation, lactation of young, molting, defence of breeding females). The ability to suppress the stress response may permit fasting animals to utilize fat stores and spare protein by preventing the catabolic, protein-mobilizing effects of GCs. King penguins in the Antarctic can fast for up to 3–4 mo while incubating and molting (Cherel *et al.*, 1988*a*; Cherel *et al.*, 1988*b*). Polar bears (Stirling, 2002), Svalbard reindeer (*R. t. platyrhynchus*) (Pond, 1998), and Svalbard ptarmigan (*Lagopus mutus hyperboreus*) (Blix, 1989) rely on fat reserves as energy stores during the winter period. They first prepare for the fast by a hyperphagic phase in which body fat stores increase. They then adjust to long-term fasting by mobilizing the fat stores and sparing body proteins (Bernard *et al.*, 2003). The details of natural fasting physiology have been well worked out in male king penguins (Cherel *et al.*, 1988*a*, *b*) and these findings may indicate the pattern in other species. Fasting is characterized by three phases. During phases I and II, first glycogen stores and then lipid stores, respectively, are the sources for energy; concentrations of corticosterone, insulin, and thyroid hormone remain low. If the fast continues until lipid stores reach some critical lower limit, the birds enter phase III when protein is no longer spared. Corticosterone and glucagon concentrations now increase markedly, and because GCs promote protein mobilization, protein now becomes the main energy source. The net result is muscle wasting. The decline in body condition of polar bears in the western Hudson Bay near Churchill, Manitoba (Stirling and Derocher, 1993; Stirling *et al.*, 1999) over the last decade owing to the effects of global warming may be indicative of animals approaching this muscle wasting phase. When the sea ice melts and the ability to hunt seals stops, polar bears in this region spend their summers on the shore and fast. Because the sea ice is melting earlier and freezing later, the bears must fast for a longer period than they are adapted to and hence condition is declining. This decline is associated with reduced female condition and declining natality (Derocher and Stirling, 1995).

ADAPTATIONS FOR REPRODUCING IN NORTHERN ENVIRONMENTS

The necessity of reproduction during a short summer places critical demands on northern birds and mammals at a time when they may simultaneously have to deal with unpredictable contingencies such as severe weather or predators that may compromise the reproduction. I will give three examples of solutions that northern species have evolved to maximize their fitness. The first, of snowshoe hares experiencing the stressor of chronic high predation risk during the decline of the 10-year cycle, reinforces the conventional understanding of how the HPA axis normally works: when animals are subjected to a chronic stressor, reproduction is inhibited or reduced. The other two examples illustrate specific adaptations of the stress axis to get around the problem of potentially being chronically stressed and yet continuing to reproduce. Some Arctic breeding birds continue to reproduce by not responding to stressors that would normally cause a strong activation of the stress response and an inhibition of reproduction. In contrast, breeding male Arctic ground squirrels continue to reproduce in spite of the fact that they are chronically stressed by the intense intrasexual competition. In the first example, animals trade off reproduction for survival; in the latter two, they may trade off survival for reproduction.

Snowshoe hares exhibit 10-year population cycles throughout the boreal forests of North America and these cycles have been occurring for at least the last 300 years (Krebs *et al.*, 2001). During the 2–3 year period of population declines, virtually every hare that dies is killed by a predator and all the physiological evidence indicates that during this time, they are chronically stressed by the high predator threat. Using the hormonal-challenge protocol, Boonstra *et al.* (1998) found that in contrast to the increase phase of the population cycle, hares during the decline phase had higher concentrations of free cortisol (Fig. 3), reduced GC binding capacity (CBG—a binding carrier protein in plasma is normally present in moderate concentrations and limits the amount of free GCs in circulation), reduced testosterone response, reduced body condition, reduced white blood cell count, increased overwinter body mass loss, and increased glucose mobilization (Fig. 3). The higher concentrations of glucose released in response to the ACTH injection in decline hares indicate that they are increasing liver production and storage of glucose as glycogen in response to chronic stress by enhancing the liver's capacity for gluconeogenesis (Miller and Tyrrell, 1995). This comes at the expense of peripheral tissues by de-

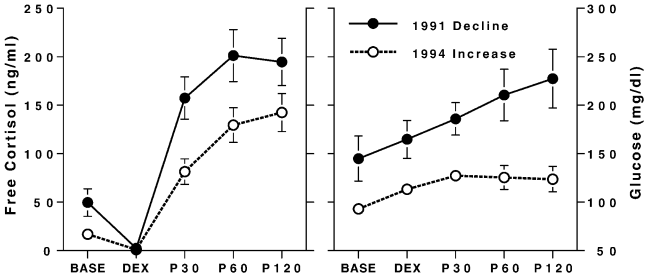

FIG. 3. Effects of the hormonal-challenge protocol (means ± 1 SE) on free-living snowshoe hares (both sexes combined) from the southwestern Yukon during the first year of the population decline (1991) and the first year of the population increase (1994). The left panel shows the changes over time in free cortisol: Base indicates concentrations at the initial bleed; DEX indicates those 2 hr after the dexamethasone (a GC analogue) injection; and P30, P60, and P120 indicates those concentrations 30, 60, and 120 min respectively after the ACTH injection. The right panel shows the changes over time in glucose concentrations at these same points (modified from Boonstra *et al.*, 1998).

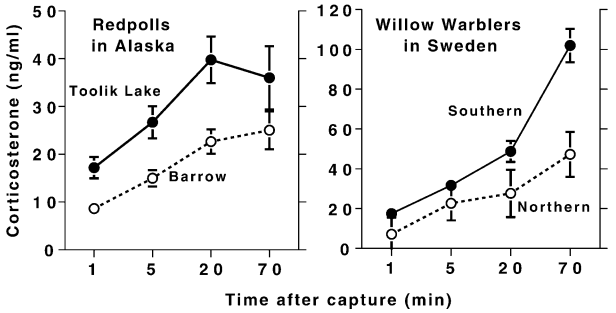

FIG. 4. Changes in total plasma corticosterone concentrations following the capture-challenge protocol in free-living males songbirds in southern and northern regions of their breeding range (means ± 1 SE). The left panel shows the changes in plasma corticosterone concentrations of breeding redpolls in June in Alaska from Toolik Lake (69°N) and from Barrow (71°N), Alaska (modified from Wingfield *et al.*, 1994). The right panel shows the effects of these changes in breeding willow warblers from southern Sweden (Göteborg 57°42′N) and from northern Sweden (Ammarnäs 63°58′N) (modified from Silverin *et al.*, 1997).

creasing their glucose uptake and utilization, by the release of gluconeogenic substrate from peripheral tissues, and by increasing protein breakdown and decreasing protein synthesis (Fig. 1). These responses are expected of an animal under chronic stress (Sapolsky, 2002) and thus hares have not evolved a modulation of HPA axis adaptation to meet the challenge of this recurrent stressor. Thus hares appear to be making the best of a bad situation, focusing all their energies on short-term survival. However, the cost appears to be a significant reduction in reproduction to <40% of that found in increase phase (7.0 young/female/summer during the decline versus 18.9 young/female/summer during the increase—Stefan and Krebs, 2001). Thus, an attack by a predator may be one environmental factor that always requires a complete mobilization of the ''flight or fight'' stress response and when the frequency or threat of these attacks reaches a certain threshold, continuous activation of the stress axis precipitates the typical negative effects of chronic stress. However, in contrast to the expectation of Selye (1971) that HPA exhaustion should be the ultimate end result of chronic stress, adrenal exhaustion was never observed.

Birds breeding at high latitudes or at high altitudes are confronted by having to reproduce during a short growing season while at the same time having to cope with a unpredictable environment which can produce severe spring storms. The normal reaction to such weather would be a stress response, focusing body resources on survival. However, this would inhibit reproduction. Wingfield (1994) proposed that species breeding in such environments suppress the adrenocortical response to such acute stressors, thus enhancing their chances for reproductive success. Figure 4 gives evidence to support this hypothesis: within some species, more northernly breeding populations during the breeding season respond less to the capture-stress protocol than do populations breeding further south (Romero *et al.*, 2000; Wingfield and Hunt, 2002). Recent evidence suggests that the modulation of the stress response may occur not only between populations, but also with individuals with the strength of the response being lowered when reproductive investment or effort is greatest (Holberton and Wingfield, 2003). However, the generality of this modulation is tempered by two findings. First, if environmental conditions become chronic, the normal stress response may become activated and reproduction is traded off for survival. Astheimer *et al.* (1995) found that in the Lapland longspurs (*Calcarius lapponicus*) at Toolik Lake, Alaska a prolonged snow storm caused nest and territory abandonment and those birds recaptured subsequently had greatly increased corticosterone concentrations relative to the same birds before the storm. Second, not all species living at high latitudes show a reduced stress response during the breeding season (Wingfield *et al.*, 1995): some species such as the rock ptarmigan (*Lagopus mutus*) and red phalarope (*Phalaropus fulicaria*), when challenged with a capture-stress protocol, showed corticosterone concentrations that were similar to those of other species at lower latitudes (though the exact stage of breeding may not have been determined in these studies). The interpretation of the response to stressors during various phases of the annual breeding cycle of northern birds may be modulated by parental effort between and within the sexes, by concentrations of the GC binding capacity (CBG—see above), and by variation in the sensitivity the HPA axis at either the level of the brain or the adrenals (*e.g.*, Romero *et al.*, 1998; Wingfield and Hunt, 2002).

Arctic ground squirrels are found throughout the tundra and alpine areas of mainland Canada, into the boreal forests of northwestern Canada, and throughout Alaska (Karels and Boonstra, 2000). They are obligate hibernators, emerging above ground from 7–8 months of hibernation in early to mid-April, with males appearing about 1–2 weeks before females. Mating is

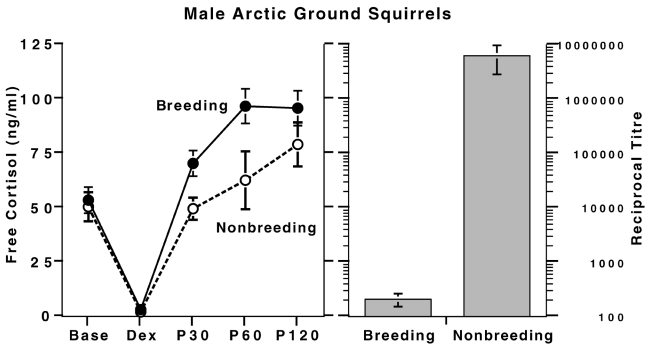

FIG. 5. Effects of the hormonal-challenge protocol and immunocompetence challenge (means ± 1 SE) on breeding (May) and nonbreeding (August) adult male Arctic ground squirrels from the Yukon. Free-living males were captured in live-traps and taken to a central site where the challenge was performed. The left panel shows the changes over time in free cortisol: Base indicates concentrations at the initial bleed; DEX indicates those 2 hr after the dexamethasone (a GC analogue) injection; and P30, P60, and P120 indicates those concentrations 30, 60, and 120 min respectively after the ACTH injection. The right panel shows the antibody titer response based on hemagglutination 7 days after sheep red blood cells were injected subcutaneously (modified from Boonstra *et al.*, 2001).

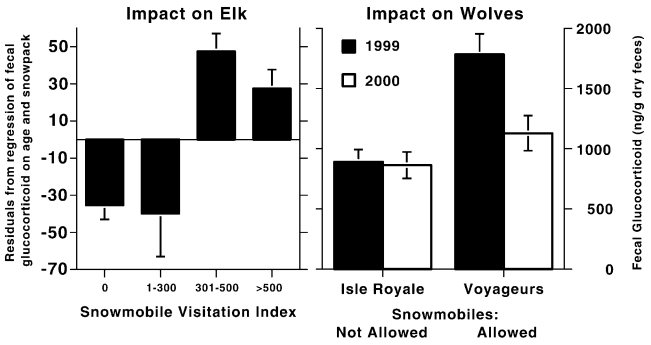

FIG. 6. Impact of snowmobiles on stress in wildlife. The left panel shows the fecal GC concentrations of adult female elk of known age as a function of the daily number of snowmobiles entering the area. GC concentrations were adjusted for age of females and snow depth and thus the ordinate shows the residuals from the regression of GC concentrations on these two factors. The right panel shows the fecal GC concentrations in wolves from Isle Royale, where no snowmobiles were allowed, and from Vogageurs, where snowmobiles were allowed (modified from Creel *et al.*, 2002).

highly synchronous, with all females being bred within 2–3 weeks of emergence. During this time, males fight intensely for the opportunity to mate, with serious injuries such as loss of eyes and gaping head wounds being frequent. Breeding males show evidence of a hormonal system geared to maximizing the chances of reproductive success irrespective of its long-term survival costs: they have the highest concentration of free cortisol (Fig. 5), the lowest GC binding capacity, the poorest ability to respond to an antigen challenge (Fig. 5), and testosterone concentrations which go up, not down, when challenged by a stressor (Boonstra *et al.*, 2001). Normally, a stressor causes an inhibition of the gonadal axis and thus testosterone levels should decline. In contrast these increasing testosterone levels when subjected to stressors suggest that male squirrels will not back down when fighting with other males, essentially ''upping the ante,'' and this may result in their severe injuries. About half of these males disappear during or shortly after the breeding season. Thus HPA axis and the immune response of breeding males are severely compromised relative to males at other times. Similar life history constraints (a short breeding season and low between-year survival) may select for a similar adaptive stress response in other mammals (Boonstra and Boag, 1992).

IMPACTS OF HUMAN ACTIVITIES ON THE STRESS AXIS IN WILDLIFE

Local and regional impacts

Birds and mammals may be either directly or indirectly stressed by the local and regional activities of humans. Depending on the duration and timing of these activities (during the animal's breeding versus nonbreeding season), these stressors may have individual or population consequences. Three examples highlight the potential for stressor impacts. First, snowmobiles in winter and ATVs (all terrain vehicles) in summer are major terrestrial modes of motorized transport in the north. Wildlife exposed to the noise of these machines may be stressed by them. Creel *et al.* (2002) measured fecal GC concentrations in elk (*Cervus elaphus*) and wolves in U.S. national parks exposed to different levels of snowmobile activity (Fig. 6). Both elk and wolf populations had higher concentrations of fecal GCs in areas and at times of heavier snowmobile use. However, Creel *et al.* were not able to detect any negative impact on the population dynamics of these two species from the current levels of snowmobile activity.

Second, activities associated with logging (felling of trees and logging truck traffic) may stress animal populations living nearby. In nesting Northern spotted owls (*Strix occidentalis*), an endangered species in the Pacific northwest, fecal GC concentrations in males were positively correlated with these logging practices (Wasser *et al.*, 1997).

Third, hunting wild game is a major activity throughout the north. Hunting may cause short-term stresses to animals in the same way that a short-duration predator attack stresses prey and elicit a short-term, acute response. However, hunts that are of long duration, occurring over many hours or longer, or to which the animal has no natural equivalent (*e.g.*, large predators being pursued as prey animals) may be deleterious and result in chronic stress. Cougars (*Puma concolor*) that had been repeatedly chased by dogs over a series of weeks as part of a ''nonconsumptive hunting'' strategy showed a diminished response to an ACTH challenge in comparison with control animals (Harlow *et al.*, 1992), suggesting that they were suffering from the effects of chronic stress. One of the methods of hunting red deer in Britain (Bateson and Bradshaw, 1997) and moose in Sweden (Ball *et al.*, 1997) has involved pursuit by dogs. Relative to red

deer shot without the pursuit, those hunted with dogs had cortisol concentrations up to 70% higher, disruption of muscle tissue, exhaustion of glycogen reserves, and breakdown of red blood cells (Bateson and Bradshaw, 1997). The researchers estimated that up to 8% of the deer that succeeded in escaping the pursuing dogs subsequently died from the effects of the hunt. Thus in wildlife management related to hunting or to other human activities, care should be taken to avoid activities causing chronic or extreme stresses.

Global impacts

Two long term, persistent, and pervasive changes are affecting northern environments simultaneously: global climate change and contamination of virtually all natural habitats by chemicals of anthropogenic origin (*e.g.*, persistent organochlorine pollutants [Goldman, 1997] such as PCBs, DDT, and hexachlorocyclohexanes; polynuclear aromatic hydrocarbons; heavy metals, artificial radionuclides). Both changes may affect or compromise the HPA axis of northern birds and mammals that may then cascade into population, community, and ecosystem effects.

Climate change

Over the last 100 years, the earth's climate has warmed approximately 0.6°C and this rate of increase is the most rapid of that seen in the last 1,000 years (Climate Change, 2001). Computer model projections indicate that relative to 1990, the temperature by 2100 will increase between 1.4 and 5.8°C. Organisms could respond to this warming by changes in physiology, behavior, and morphology, by changes in population density, by shifts in range distributions either poleward or upward in elevation, by changes in the timing of life history events such as migration or initiation of breeding, and by changes in gene frequencies (Hughes, 2000; Walther *et al.*, 2002; Root *et al.*, 2003). Animal and plant populations have already shown marked responses to this increase in global temperature. From a meta-analysis of a large number of species or groups of species (Parmesan and Yoye, 2003), range shifts averaging 6.1 km per decade over the last 50 years toward the poles (or meters per decade upward) and advancement of spring events averaging 2.3 days per decade were found. A similar analysis found that the average shifts in spring phenology (breeding or blooming) in temperate species was 5.1 days earlier in a decade (Root *et al.*, 2003). Given the projections of a much larger increase in temperature this century relative to the previous one and that temperature increases will be exacerbated at high latitudes (Climate Change, 2001), northern species and their environments are likely to be under severe pressure. Shifts in range distribution will be more readily accomplished for the migratory bird species (Boyd and Madsen, 1997) and some mobile groups of mammals (*e.g.*, caribou and hares, Klein, 1999). However for mammal species that are more sedentary (*e.g.*, Arctic ground squirrels), the rapidity of global warming may preclude or delay significant dispersal to capitalize on these changes (Peters and Lovejoy, 1992).

From the standpoint of the HPA axis, the critical question is whether northern bird and mammal species have either the phenotypic plasticity, the genotypic variability, or both to adapt to the new reality of higher temperatures or greater unpredictability caused by global warming. Realé *et al.* (2003) show that both act to result in earlier reproduction in Yukon red squirrels in response to earlier springs. Depending on how changes in weather translate into changes in the environment that the animals experience, the HPA axis may have a role to play in permitting them to meet this new challenge. We do not know the answer to this for most species, though we have a greater insight on this in birds than in mammals. In birds, many species exhibit between-population variation over a latitudinal cline in responsiveness to standardized stressors at certain phases of the reproductive cycle (Wingfield and Romero, 2001; Wingfield and Hunt, 2002). This variation and their ability to move large distances rapidly, may allow them to respond quickly to changes in environmental conditions. For most northern mammals, there is a paucity of even baseline endocrinological information and all studies to date have focused on within-population variation in HPA responsiveness. For example, red squirrels have an enormous distributional range throughout the length and breadth of northern and western North America, yet have been subject to only one study on the stress axis in one area (Boonstra and McColl, 2000). As well, the stress axis may play no role to permit adaptation depending on the timing of climate-induced changes. For example, reduction in winter snow cover when Arctic ground squirrels are hibernating, may both reduce female overwinter survival in alpine areas (Gillis, 2003) and reduce female reproduction in the next breeding season in the boreal forest. Karels and Boonstra (2000) found that variation in winter snow cover acted as a density independent factor: low snow cover resulted in poorer condition of females at emergence from hibernation and reduced their weaning success in late spring-early summer. Thus changes in the HPA axis will be unlikey to help these animals cope with declining conditions if the latter occur during hibernation. Finally, since the smaller mammals are reasonably sedentary, coping with climate change will depend on the speed with which it occurs relative to their speed of dispersal.

Northern contaminants

The second major factor affecting the north is the transfer to these regions of large variety of anthropogenically produced substances. Canada has been trying to understand their distribution, movement, and impact for the past decade since initiating the Canadian Northern Contaminants Program in 1991 (de March *et al.*, 1997; de Wit *et al.*, 2003). Many of these contaminants may be endocrine disrupting compounds (EDC). These are exogenous substances or mixtures of them that al-

ter the function(s) of the endocrine system and consequently causes adverse health effects in an intact organism and its progeny or populations (Lister and Van der Kraak, 2001). Their modes of action are incredibly complex and diverse, with some mimicking or inhibiting the actions of hormones through interaction with hormone receptors and mechanisms of action, others altering the synthesis of a hormone or its receptor, and others altering the rate of metabolism and/or excretion of a hormone (Norris, 2000).

The major focus of research up to the present time has been on the impacts of EDCs on reproductive dysfunction and related areas (Jimenez, 1997; Crews *et al.*, 2000; Iguchi and Sato, 2000), with relatively little attention being directed toward understanding their impact on the HPA axis. I summarize some of this search. Throughout the north, PCBs are a widespread contaminant and bioaccumulate up the food chain (Kelly and Gobas, 2001). In the field, high body burdens of PCBs and of DDT are known to be correlated with adrenal hyperplasia, necrosis, and/or hyperadrenocortism (de March *et al.*, 1997). In the laboratory, a number of contaminants have severe effects on the HPA axis. Repeated exposure of rats to PCBs cause elevated basal corticosterone concentrations (Miller *et al.*, 1993). The mechanism may involve the GC receptor (GR, Fig. 1), a critical component in the regulation of the limbic system and the HPA axis (Fig. 1). Methylsulfonyl PCBs will bind to the GR (Fig. 1), competing for access to the binding site with the artificial GC, dexamethasone, and thus possibly also with natural GCs (Johansson *et al.*, 1998). Thus blocking the GR could limit the stress response to a stressor. Hyperadrenocortism occurs in Baltic seal populations and this is possibly related to the high levels of PCBs and DDT they carry (Bergman, 1999). Dioxin (2,3,7,8-tetrachlorodibenzo-p-dioxin) is another widespread environmental contaminant found in the north (de March *et al.*, 1997) and has severe effects on the HPA axis. In laboratory cynomolgus monkeys (*Macaca fascicularis*), it disrupted the HPA axis by increasing levels of CRH mRNA in the hypothalamus and by increasing cortisol concentrations in plasma (Shridhar *et al.*, 2001). In rats, it results in altered blood concentrations of ACTH (Bestervelt *et al.*, 1998) and of corticosterone (Gorski *et al.*, 1988).

The impact of contaminants on the inability of an organism to respond successfully to environmental stressors may only become obvious when such a challenge occurs. Thus, simply examining baseline concentrations of GCs may not be enough. The only example I can find of this comes from fish. Norris (2000) found that in wild populations of brown trout (*Salmo trutta*) exposed to the heavy metals zinc and cadmium (cadmium acts as an EDC in vertebrates), baseline concentrations of cortisol did not differ between exposed animals and controls. However when both groups were challenged with a stressor, exposed fish were unable to reestablish homeostasis rapidly after removal of the stressor. Thus, imposing a challenge is an effective way to assess whether contaminants have compromised the ability of the HPA axis to respond. In summary, the stress axis is clearly vulnerable to EDCs but a great deal needs to be done in both the field and laboratory to assess their impact at both the individual and population level.

CONCLUSIONS AND NEED FOR FUTURE STUDY

The goal of individuals is to maximize life-time reproductive fitness and the functioning of the stress axis is key to making this happen. Coping with change is a key requirement for survival and reproduction both from both a short-term, ecological perspective and a long-term, evolutionary perspective and the stress axis is a critical one in this process. It is multi-tasking throughout the life of birds and mammals, but is subject to modification and permanent change if environmental conditions dictate. There is tendency to think of this axis only in relation to the response of the body to short-term stressors, yet it plays a key role all the time—winter and summer, in and out of breeding condition—to both carry out the daily functions of living and to cope with environmental challenges. The overview of the various solutions that birds and mammals use to deal with northern challenges high light two things. First, we have only scratched the surface in our understanding of how the stress axis functions to equip homeotherms for life in the north, with that in birds being deeper than that in mammals. Thus the broad-scale patterns are only slowly emerging. Second, the degree to which these solutions are genotypic or phenotypic and thus able to respond to long-term, directional change such as global warming, is unknown and this may limit their ability to respond. Thus studies in natural populations examining the causes of variation in the stress axis and its response to challenges are needed.

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